

Spiomenia spiculata, Gen. et Sp. Nov. (Aplacophora: Neomeniomorpha) Collected from the Deep Waters of the West European Basin

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Abstract. *Spiomenia spiculata* gen. et sp. nov. was collected from deep waters of the West European Basin at depths from 1600 to 4400 meters. *Spiomenia* is placed in the family Simrothiellidae on the basis of the presence of distichous radular bars, which have many denticles during some point in ontogeny, and paired anteroventral radular pockets. It is separated from other genera in the family by the absence of skeletal spicules, denticulation of the radula, and presence of captate upright spicules.

INTRODUCTION

Spiomenia gen. nov. is a genus of neomenioid aplacophoran mollusk which occurs in the benthos throughout the deep Atlantic. It is placed in the Family Simrothiellidae based on the presence of a radula with distichous bars and paired anteroventral radular pockets. The Family Simrothiellidae at present comprises nine other genera of which four are monotypic (Table 1). Of these, three are described from a single sectioned specimen, and information concerning the spicules and radulae are not reported in detail. There are many incongruent morphological characters within this family and it is probably not monophyletic. For example, *Helicoradomenia* Scheltema & Kuzirian, 1991, and *Sialoherpia* Salvini-Plawen, 1978, possess solid epidermal spicules, but spicules are hollow in other genera. *Uncimienia* Nierstrasz, 1903, was described as having both captate spicules similar to those of *Spiomenia* and barbed spicules similar to neomenioids in the family Pruvotinidae. *Uncimienia* was also reported to lack a radula. All other genera in the family lack barbed spicules and possess a radula.

MATERIALS AND METHODS

Specimens (105) were collected from several localities in the West European Basin during the 1976 French sponsored INCAL/CENTOB cruise (Table 2). Type specimens are deposited in the Muséum National d'Histoire Naturelle (MNHM) Paris, France.

Dissections

Lengths were measured along the midline in lateral view. Width measurements were made with the specimen

oriented dorsoventrally. Radulae, epidermal spicules, and copulatory spicules were dissected from three animals; six were sectioned for histology. Radulae were dissected by placing the anterior half of the animal in hypochlorite solution. After the tissue was dissolved, the radula was removed with the remaining anterior spicules and washed in distilled water overnight. Spicules were placed on a glass slide, air dried, and permanently mounted in Histomount®. Radulae were first observed in a drop of glycerine for camera lucida drawing, then washed in distilled water and permanently mounted in CMCP-10® for drawing under oil immersion. Copulatory spicules were dissociated by placing the posterior half of the animal in hypochlorite solution. After the tissue was dissolved, spicules were removed, washed in distilled water, air dried, and mounted in Histomount® for drawing under the camera lucida.

Histology

Six specimens, previously fixed in formalin and preserved in alcohol, were post-fixed overnight in zinc formalin (Presnell & Schreiber, 1997) and embedded in filtered Paraplast®. Sections were cut at 7 µm and stained with hematoxylin and eosin Y or Mallory's Trichrome and mounted in Histomount®.

Terminology and Abbreviations

Terminology and abbreviations in this paper follow those of Scheltema & Kuzirian (1991). New terms not mentioned previously in the literature, some specific to *Spiomenia* are: the *radular buttress* (BU) which is the thickened lateral portion of each radular tooth (Figure 1D, E). *Double denticle* (DD) is the lateralmost denticle on the radular tooth and is composed of two denticles fused at the base (Figure 1D). *Captate spicules* (CA) are those with small peaks at the apical end (Figure 1F).

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Table 1

Number of species presently known for each genus currently placed in the family Simrothiellidae.

Genus	Author, date	Number of species
<i>Simrothiella</i>	Pilsbry, 1898	2
<i>Cyclomenia</i>	Nierstrasz, 1902	1
<i>Kruppomenia</i>	Nierstrasz, 1903a	4*
<i>Uncimonia</i>	Nierstrasz, 1903b	2*
<i>Biserramenia</i>	Salvini-Plawen, 1968	1
<i>Birasoherpia</i>	Salvini-Plawen, 1978	1
<i>Sialoherpia</i>	Salvini-Plawen, 1978	1
<i>Helicoradomenia</i>	Scheltema & Kuzirian, 1991	3
"New Genus P"	Scheltema	3*
<i>Spiomenia</i>	new herein	4*

* Some species descriptions in manuscript.

SYSTEMATICS

Subclass NEOMENIOMORPHA Pelseneer, 1906

Family SIMROTHIELLIDAE Salvini-Plawen, 1978

Spiomenia Arnofsky, gen. nov.

Description: Spiny habitus, typically curved due to preservation, 3.5 mm or less in length; dorsofrontal sensory pit obscured by spicules; proboscis large, protrusible; mouth opening at posterior end of vestibule. Pedal pit

large; cuticle thick, thickened laterally and ventrally; spicules hollow, upright, many captate, skeletal spicules absent; radula large, longest denticles on buttress, one to many denticles lateral to the radular buttress; radula with one turn into paired anteroventral radular pockets, first-formed teeth not retained; paired ventral salivary glands large, within muscle tissue; mantle cavity with three pairs of long respiratory papillae, often extending outside mantle cavity. The two autapomorphic characteristics of the genus are: (1) possession of captate upright spicules and (2) from one to many denticles lateral to the radular buttress.

Distribution: Four species, each from geographically separated basins of the Atlantic Ocean belong to the genus *Spiomenia*; descriptions of three species remain unpublished. *Spiomenia spiculata* is described from the West European Basin (2000–4000 m). The other species are from the North American Basin (2100 m), from both the Canary and Cape Verde Basins (1600–3100 m), and from the Argentine Basin (1600–5000 m). One specimen collected from the Indian Ocean is thought to be a fifth new species, but more specimens of this form need to be collected. It is likely that *Spiomenia* species are distributed throughout the deep ocean basins.

Etymology: *Spio* from Greek meaning sea nymph, *menia* from Greek meaning moon, a typical generic ending for neomeniomorph aplacophorans.

Table 2

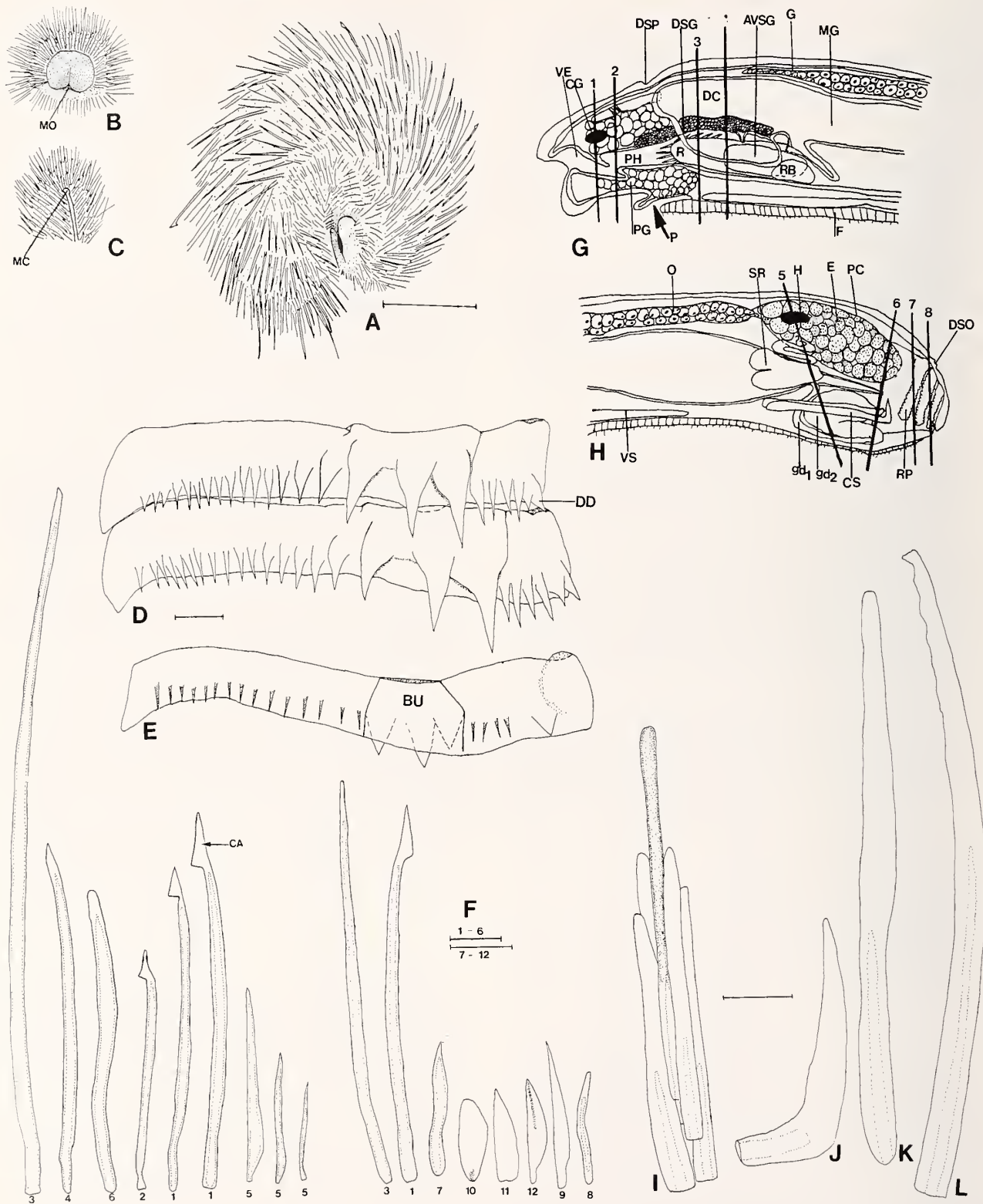
Locality information for *Spiomenia spiculata* collected from the West European Basin during the INCAL/CENTOB cruise.

Equipment*	Latitude north		Longitude west		Depth (m)	Date collected	No. of specimens	
	Degrees	Minutes	Degrees	Minutes				
CP-01	TR	57	57.7	10	55	2040	16/07/76	2
CP-02	TR	57	58.4	10	42.8	2091	16/07/76	1
CP-05	TR	55	0.4	12	29.4	2884	19/07/76	4
CP-06	TR	55	2.3	12	40.3	2888	19/07/76	8
CP-07	TR	55	3.4	12	46.2	2895	20/07/76	8
CP-08	TR	50	14.7	13	13.5	2644	27/07/76	9
CP-09	TR	50	15.4	13	15.8	2659	27/07/76	5
DS-02	ES	57	58.8	10	48.5	2081	16/07/76	10
DS-05	ES	56	28.1	11	11.7	2503	18/07/76	12
DS-06	ES	56	26.6	11	10.5	2494	18/07/76	4
DS-07	ES	55	0.7	12	31	2884	19/07/76	1
DS-08	ES	55	2.0	12	34.6	2891	19/07/76	3
DS-09**	ES	55	7.7	12	52.6	2897	20/07/76	17
OS-02	ES	50	14.4	13	10.9	2634	30/07/76	4
OS-06	ES	47	27.3	9	36.2	4307	09/08/76	2
WS-01	TR	50	19.4	13	8.1	2550	30/07/76	12
WS-02	TR	50	19.3	12	55.8	2498	30/07/76	3

Total = 105

* TR = Trawl, ES = Epibenthic Sled.

** = Type locality.



Spiomenia spiculata Arnofsky, sp. nov.

(Figures 1–3)

Material examined: 105 individuals from the Western European Basin (2040 m–4307 m); See Table 2.

Holotype (Figures 1A–C, 2J): 2.3 mm long, anterior width 0.7 mm, midbody width 0.7 mm, posterior width 0.6 mm. INCAL (CENTOB) Loc. 4, DS-09, 55°7.7'N, 12°52.5'W, 2897 m.

Numbered paratypes: Paratype no. 1: INCAL (CENTOB) Loc. 4, DS-09, 55°7.7'N, 12°52.5'W, 2897 m, dissected specimen, anterior and posterior spicules and radula.

Paratype no. 2: INCAL (CENTOB) Loc. 4, DS-09, 55°7.7'N, 12°52.5'W, 2897 m, whole animal.

Paratype no. 3: INCAL (CENTOB) Loc. 4, DS-09, 55°7.7'N, 12°52.5'W, 2897 m, dissected specimen, anterior spicules and copulatory spicules.

Paratype no. 4*: INCAL (CENTOB) Loc. 4, DS-09, 55°7.7'N, 12°52.5'W, 2897 m, histologic sections (seven slides).

Paratype no. 5: INCAL (CENTOB) Loc. 4, DS-09, 55°7.7'N, 12°52.5'W, 2897 m, histologic sections (15 slides).

Paratype no. 6*: INCAL (CENTOB) Loc. 4, DS-09, 55°7.7'N, 12°52.5'W, 2897 m, histologic sections (eight slides).

Paratype no. 7: INCAL (CENTOB) Loc. 4, DS-05, 56°28.1'N, 11°11.7'W, 2503 m histologic sections (10 slides).

Paratype no. 8*: Loc. 4, DS-09, 55°7.7'N, 12°52.5'W, 2897 m, histologic sections (five slides).

Paratype no. 9*: Loc. 4, DS-09, 55°7.7'N, 12°52.5'W, 2897 m dissected specimen, radula and anterior spicules.

Lots sent to MNMH for type series OS-06; 4307 m, DS-07; 2884 m, DS-08; 2891 m, and type locality DS-09; 2897 m.

Lots excluded from type series for further investigation: CP-01; 2040 m, CP-02; 2091 m, CP-05; 2884 m, CP-06; 2888 m, CP-07; 2895 m, CP-082644 m, CP-09; 2659 m, DS-02; 2081 m, DS-05; 2503 m, DS-06; 2494 m, OS-02; 4829 m, WS-01; 2550 m, WS-02; 2498 m.*

Diagnosis: Length to 3.1 mm with a mean size of 1.8 mm (n = 105). Narrowest posteriorly; mean index (height:width) at midbody 1:1. Length of cap of large captate spicules 38–48 μ and for small captate spicules 10–30 μ m. Radula with single turn into paired anteroventral radular pockets; five denticles lateral to the buttress, lateralmost being a double denticle; formula 22–25 \times 1: 1, 20–23 denticles per tooth (Figures 1D, E, 2J). Two types of copulatory spicules in paired groups protruding through the mantle cavity opening (Figure 3D).

External anatomy and hard parts: Body curved, posterior end tapering slightly, usually widest at midsection (Figure 1A–C). Dorsofrontal sensory pit, dorsoterminal sense organ and mantle cavity opening obstructed by spicules, difficult to discern. Longest epidermal spicules posterior, near mantle cavity opening. Spicules of nine types (Figure 1F): Type 1, large, captate, 350–450 μ m in length, up to 10 μ m in width, hollow to cap; recurved 50 μ m from base. Type 2, smaller, captate, 190–240 μ m in length, 6 μ m in width, hollow to cap. Type 3, large, long, slightly curved, obliquely truncate at apical end, 325–800 μ m in length, up to 15 μ m in width; recurved 35 μ m

* Numbered paratypes dissected or histologically sectioned excluded from type series: Paratypes nos. 4, 6, 8, and 9 INCAL (CENTOB) Loc. 4, DS-09, 55°7.7'N, 12°52.5'W, 2897 m.

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Figure 1

Spiomenia spiculata Arnofsky, gen. et sp. nov. A–C: Holotype. A. Entire, showing orientation of spicules. B. Anterior end, frontal view showing opening of mouth. C. Posterior end, ventral view, oval-shaped mantle cavity opening obscured by spicules. D–E. Paratype no. 1. Two adjacent teeth of radula, lateral to right. E. Single radular tooth, view from beneath radular membrane showing thickened lateral buttress. F. Epidermal spicules from paratypes nos. 1, 2, and 3: Types 1–6 found both anteriorly and posteriorly, largest of type 3 found near mantle cavity opening, types 7–9 found posteriorly, and types 10, 11, and 12 found ventrally beside pedal groove. G, H. Schematic diagram from histologic sections of two individuals: G. Anterior end to midsection (paratype no. 5). H. Midsection to posterior end (paratype no. 7): transverse sections 1–4 are keyed to sections A–D in Figure 2; transverse sections 5–8 are keyed to sections A–D in Figure 3. I, K. Accessory copulatory spicules, paratype no. 1. I–L. Paratype no. 3. I. *In situ* showing arrangement accessory spicules around mantle cavity opening. Stippling indicates abrasion. J and L. Copulatory spicules. J. Type 1 with sharp bend, remaining hollow portion broken during dissection. K. Accessory copulatory spicule. L. Type 3 found with type 1 spicule in copulatory spicule pocket. Key: BU, buttress; CA, captate spicule; CG, cerebral ganglion; CS, copulatory spicule pocket; DC, dorsal cecum; DD, double denticle; DSO, dorsoterminal sense organ; DSP, dorsofrontal sensory pit; E, eggs; Gd₁, upper gametoduct; Gd₂, lower gametoduct; H, heart; MC, mantle cavity; MG, midgut; MO, mouth; O, oocyte; P, pedal pit; PC, pericardial cavity; PG, pedal gland; PH, pharynx; RB, radula bolster; RP, respiratory papillae; SR, seminal receptacle; VE, vestibule; VS, ventral sinus; VSG, ventral salivary gland. Scale bars: A, B, C = 500 μ m; D, E = 10 μ m; F top scale bar for spicules 1–6 = 50 μ m, bottom scale bar for spicules 7–12 = 25 μ m. I–L scale bar = 30 μ m.

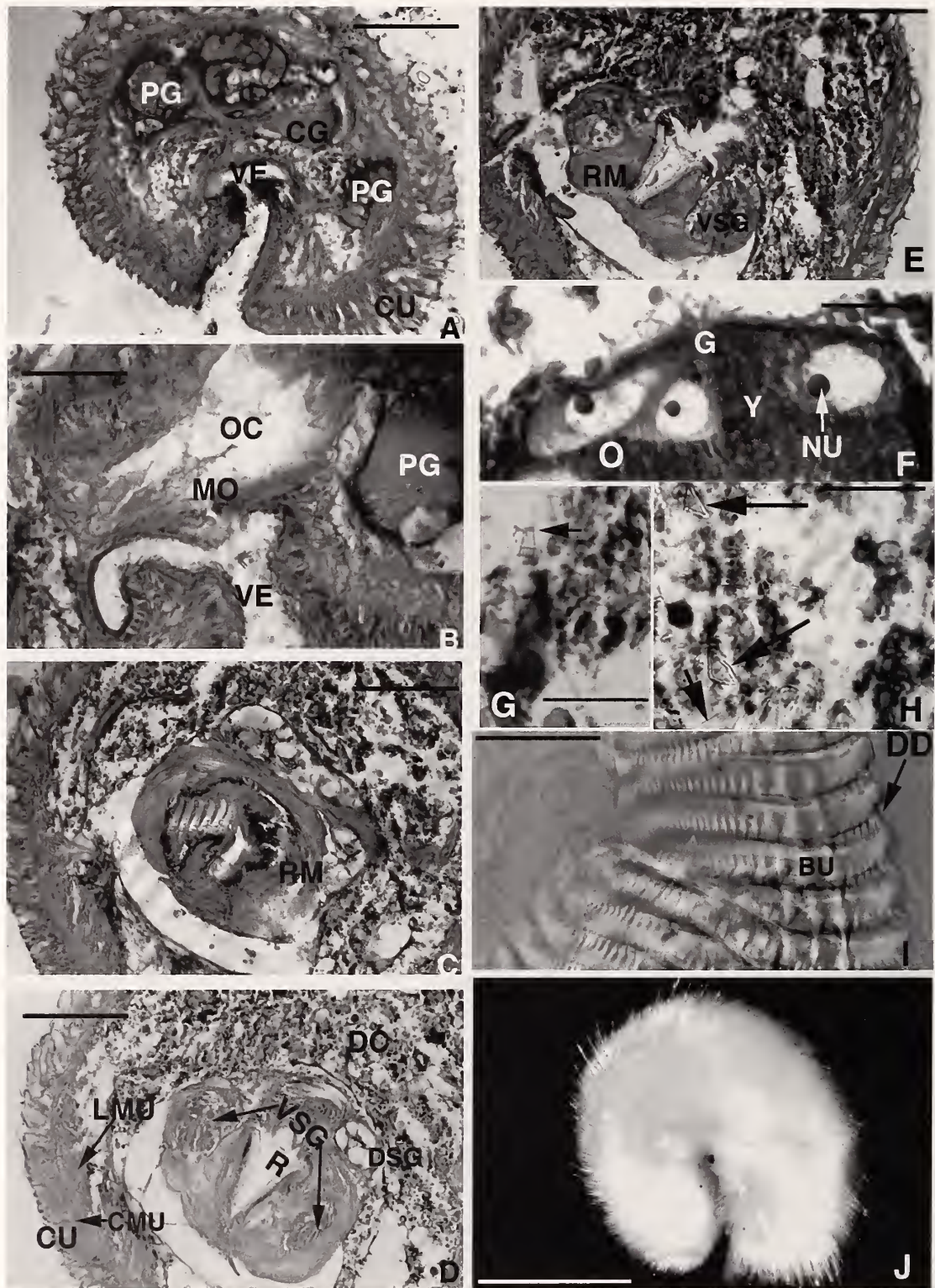


Figure 2

Spiomenia spiculata Arnofsky, gen. et sp. nov. A-E and G-H Paratype no. 5. A-D. Transverse histologic sections 1 to 4 respectively of Figure 1G. A. Section 1 through cerebral ganglion, vestibulum, and pedal gland. B. Section

from base; apical end solid at tip for 20 μm . Type 4, slightly curved, 275–310 μm long, 10 μm in width, bend at 25 μm from base; apical end solid at tip for 25 μm . Type 5, spicule length 75–175 μm in length; widest 20 μm from base, 10–15 μm wide; apical end solid at tip for 10 μm . Type 6, “S”-shaped spicule 220–240 μm in length, 15 μm in width, rounded, solid apical end 25 μm long, recurved at 75 μm from base. Type 7, recurved, apical end pointed, 54 μm in length, 6 μm in width. Type 8, small “S”-shaped spicule, pointed at apical end, 40–50 μm long, 5 μm in width. Type 9, sword-shaped, solid, found near pedal groove, widest 12 μm from base, 55–65 μm in length, 6 μm in width. Pedal groove spicules solid with three types. Type 10, oval, with small thickened portion at base, length 30–40 μm , 12 μm in width. Type 11, triangular, solid, 35–45 μm long, 9 μm in width. Type 12, solid, curved with thin basal end, ranging from 50–60 μm in length, up to 8 μm in width. Copulatory spicules of two types: type 1 bent and sharply pointed, 100 μm from bend, base hollow (Figure 1J); type 2 distally wavy, hollow, 280 μm in length (Figure 1L). Several accessory copulatory spicules grouped near mantle cavity opening (Figure 1I); one type, long, hollow, slightly curved, length up to 250 μm (Figure 1K).

Radula morphology: Radulae from eight animals examined (Figures 1D, E, 2J). Radula distichous, formula 22–25 \times 1:1 with 20–23 denticles per tooth. Most recently formed teeth 85–90 μm in greatest dimension. Five denticles lateral to buttress, double denticle 7 μm ; single lateralmost denticles 7.5–8.5 μm . Three large denticles on buttress 13.5–16.0 μm in length. Smaller denticles medial to buttress, 15–16 in number, 0.4–8.5 μm in length on younger teeth, width of radular bar at widest portion 14 μm , rest of bar 10.6 μm .

Internal anatomy: Cuticle thickest at anterior end, thickened laterally and ventrally throughout, thinnest dorsally at midsection measuring 10 μm thick, ventral thickness measuring 40 μm . Epidermis 10–20 μm thick, with more than one type of secretory cell. Body-wall musculature well developed with longitudinal, transverse, and diagonal muscles (Figure 2D). Pedal pit lined by large secretory cells. Foot small, ventral longitudinal muscles pronounced (Figure 3A, C). Vestibular papillae absent. Oral

cavity with narrow mouth opening to vestibulum (Figure 2B). Dorsal salivary gland large and paired (Figure 2C, D). Anteroventral radular pocket as paired pouches. Radula bolsters large, radular muscles well developed (Figure 2C–E) and paired ventral salivary glands within radular musculature (Figure 2D, E). Short esophagus and single, large dorsal midgut cecum (Figure 2C–E). Oocytes nucleated in gonad anterior to pericardial cavity (Figure 2F). Gonopericardial ducts paired until just before opening into pericardial cavity. Heart free within pericardium, pericardial cavity large, filled with yolky ova, which lack a nuclear membrane or nucleolus (Figures 1H, 3A). Opening of upper pericardium into upper gametoduct not determined. Seminal receptacles bilobed, paired, opening into upper gametoducts through a narrow duct (Figure 3A). Paired upper gametoducts convoluted. Lower gametoduct single, with a lower lobe into which empty upper gametoducts (Figure 3B). Seminal vesicles are absent. Gametopore single, opening into mantle cavity below rectum. Upper wall of anterior mantle cavity filled by large, vacuolated epithelial cells (Figure 3B). Dorsoterminal sense organ small, seen only in sectioned material.

Remarks: This species has unusually large, paired, dorsal salivary glands that empty into the esophagus where the it joins with the radular sac. The ventral salivary glands are also unusual in that they are embedded within the thick layer of muscle tissue that surrounds the radula. Nematocysts were not found in the gut of the six sectioned animals (Figure 2G, H). However, diatoms and unidentified spicules, which resemble those of sponges, were found in the vestibule area and within the digestive system, suggesting that this species may not depend on cnidarians as a food source.

Retention of ova in the pericardial cavity is unusual among the Aplacophora and has not been noted in the Simrothiellidae. Oocytes have a nuclear membrane and nucleolus in the gonad; however, once ova are within the pericardial cavity, the nuclear membrane has broken down. The seminal receptacles empty into the upper gametoducts, so it may be possible that sperm travel through the upper portion of the upper gametoducts into the pericardial cavity and there fertilize the eggs. It is also possible that breakdown of the nuclear membrane pre-

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2 through oral cavity, mouth opening, and vestibulum. C. Section 3 through thick radular muscles, radula, dorsal salivary gland, and dorsal cecum. D. Section 4 through paired ventral salivary glands embedded in the thick circular muscle layers of radula; dorsal salivary gland, dorsal cecum, longitudinal and circular muscles are also indicated. E. A more posterior section through the ventral salivary glands and radula showing the radular membrane. F. Paratype no. 7. Section through gonad with yolky oocytes. G, H. Contents of midgut, diatoms indicated by arrows. I. Paratype no. 1. Radula. J. Holotype. Key: BU, buttress; CG, cerebral ganglion; CMU, circular muscle; CU, cuticle; DD, double denticle; DC, dorsal cecum; DSG, dorsal salivary gland; G, gonopericardial duct; LMU, longitudinal muscle; MO, mouth; NU, nucleolus; O, nucleus; OC, oral cavity; R, radula; RM, radular muscle; VE, vestibulum; VSG, ventral salivary gland; Y, yolk. Scale bars: A, C, D, and E = 40 μm ; B, F, G, and H, = 10 μm ; I = 40 μm ; J = 500 μm .

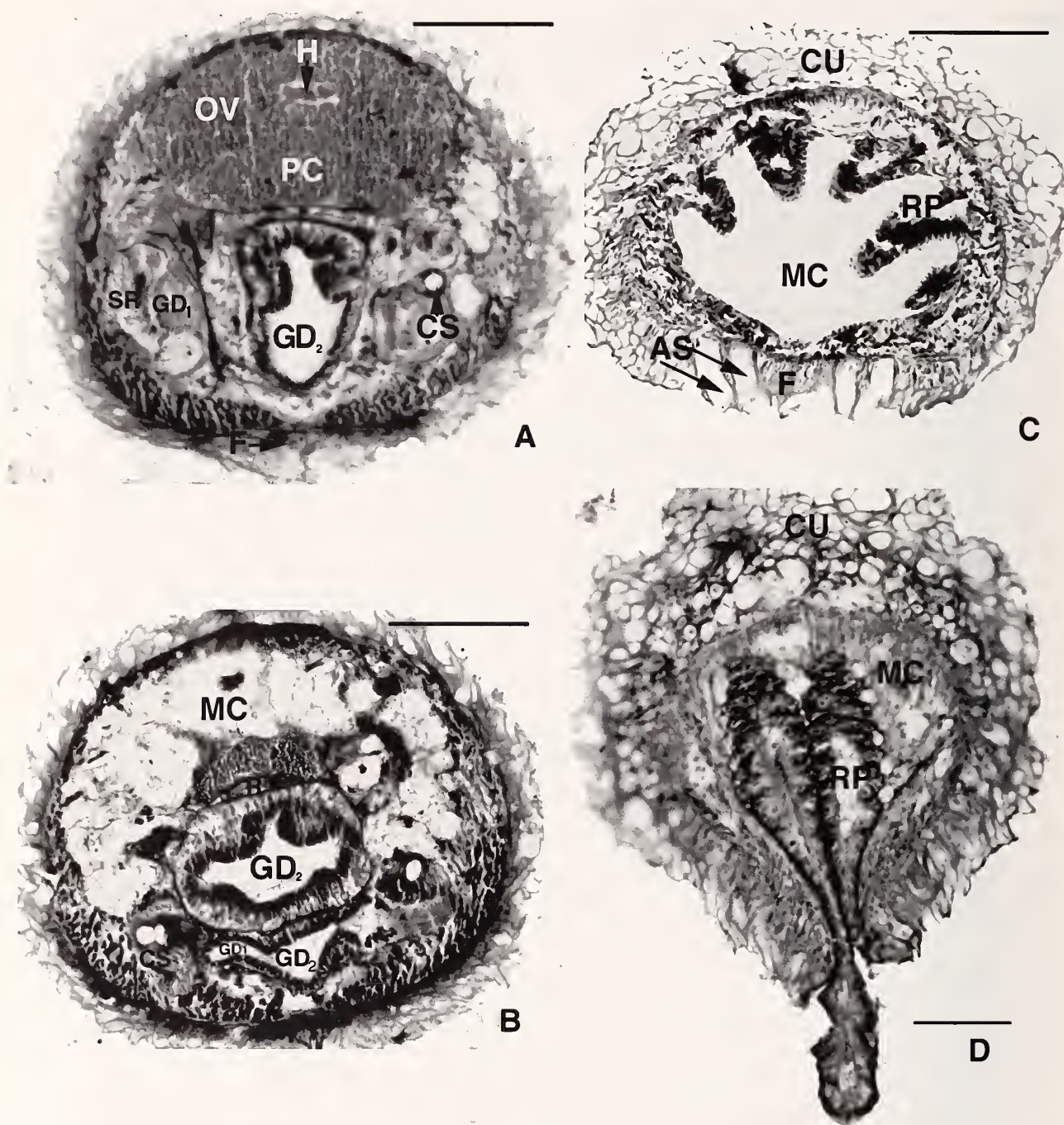


Figure 3

Spiomenia spiculata Arnofsky, gen et. sp. nov. A-D Paratype no. 7. Transverse histologic sections through posterior end; A-D represent sections 5-8 respectively of Figure 1H. A. Section 5 through seminal receptacle, lower gametoduct, upper gametoduct, heart, and pericardial cavity with large ova perhaps being brooded. B. Section 6 through rectum, mantle cavity, and connection of upper gametoduct with lower portion of lower gametoduct. C. Section 7 through mantle cavity with paired respiratory papillae, arrows, lumina of accessory copulatory spicules. D. Section 8 through posteriormost portion of mantle cavity illustrating the unusual size of the respiratory papillae. Scale bars: A-C = 40 μm, D = 10 μm. Key: AS, accessory copulatory spicules; CS, copulatory spicule pocket; CU, cuticle; F, foot; H, heart; GD₁, lower gametoduct; GD₂, upper gametoduct; MC, mantle cavity; OV, ovum; PC, pericardial cavity; RP, respiratory papillae; SR, seminal receptacle.

cedes fertilization. The origin of the upper gametoduct was not determined, as the population was comprised mostly of juveniles and it was difficult to find fully developed adults. However, it is certain that the pericardial cavity is closed at the posterior end and therefore the upper gametoduct must originate toward the anterior portion of the pericardial cavity (Figure 1H). Eggs from the pericardial cavity in living *Epimения australis* do not develop and presumably have not been fertilized. Those being brooded in the mantle cavity, where they are held together by a sticky substance, develop into larvae (Scheltema & Jebb, 1994). It may be possible that the epithelial cells within the mantle cavity of *Spionemia* also produce a mucus to bind eggs.

Relationships: *Spionemia spiculata* radulae were compared with the radulae of the nine other genera that have previously been placed in the family Simrothiellidae. Isolated radulae from *Helicoradomenia*, *Simrothiella*, *Kruppomenia*, "new genus P" (Scheltema, in manuscript), and *Uncimения* were examined, but only illustrations of the radulae drawn from histologic sections are available for *Sialoherpia*, *Birasoherpia*, *Biserramenia*, and *Cyclomenia*. All genera except *Uncimения* have distichous bars and paired anteroventral radular pockets. The radulae of genera *Simrothiella*, "new genus P," and *Spionemia* all possess a radular buttress. *Kruppomenia* also possess a denticulate, thickened, lateral portion to the radula.

The external morphology of *Spionemia* most closely resembles that of "new genus P" (as *Simrothiella* in Salvini-Plawen, 1978). However, "new genus P" is about as wide as it is long, whereas *Spionemia* is longer than wide. Both have denticulate, large radular buttresses and hollow, straight, upright spicules. In *Spionemia*, there are several denticles lateral to the buttress; these denticles are absent for "new genus P." The radula of "new genus P" is longer and has several turns into the anteroventral radular pockets, whereas radulae of *Spionemia* turn only once into the anteroventral radular pocket. Salvini-Plawen (1978) placed the family Simrothiellidae in the order Cavibelonia based on possession of hollow spicules. Scheltema & Kuzirian (1991) determined that the families of Cavibelonia vary in respect to type of radula and ventral salivary glands and in presence or absence of skeletal spicules. They also noted that the morphologies of these structures are not unique to the Cavibelonia but are found in other orders as well, and suggested that the order Cavibelonia may not be monophyletic. *Helicoradomenia* has solid upright spicules and has a very different radular

morphology from the other genera placed in this family, and it is likely that *Helicoradomenia* does not belong in Simrothiellidae. *Uncimения*, which was figured by Nierstrasz (1903b) with captate spicules similar to those of *Spionemia*, also possesses hooked spicules similar to genera that have been placed in the family Pruvotinidae. Histological sections of *Uncimения neopolitana* collected near the type locality possess a tiny radula similar to the distichous hooks of the Pruvotinidae (Arnofsky, in manuscript). In conclusion, it is likely that neither the Order Cavibelonia nor the family Simrothiellidae are monophyletic.

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